

RELATIONSHIPS AMONG RED-COCKADED WOODPECKER GROUP DENSITY, NESTLING PROVISIONING RATES, AND HABITAT

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ABSTRACT.—We examined Red-cockaded Woodpecker (*Picoides borealis*) food provisioning rates of nestlings during the 1992 and 1993 breeding seasons on the Vernon Ranger District of the Kisatchie National Forest in Louisiana. Provisioning rates were monitored at nest trees in moderate (9.8 groups/2 km radius, $n = 10$) and low (5.9 groups/2 km radius, $n = 10$) density populations. Habitat around each cluster was measured within three radii (100 m, 400 m, and 800 m) to evaluate the possible influence of habitat quality on group density and nestling provisioning rates. We tested the null hypothesis that habitat quality and provisioning rates would be similar in areas with different densities of woodpecker groups. We failed to detect differences in nestling provisioning rates between woodpecker groups in moderate versus low group densities. Woodpecker groups from areas where group densities were moderate attempted to nest significantly more often than woodpecker groups occurring in low densities. Hardwood midstory vegetation was more abundant in areas with low woodpecker group density. Old-growth pines, which are known to be important for cavity excavation, were present in habitat around cavity-tree clusters of moderate-density groups, but generally absent in areas where group density was low. Woodpecker group density may be related to hardwood midstory conditions and the abundance and spatial distribution of remnant old pines. Received 18 August 1998, accepted 9 August 1999.

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species closely associated with older-growth pine forests of the southeastern United States (U.S. Fish and Wildlife Service 1985, Walters et al. 1988). A single tree, or aggregation of cavity trees, termed the cluster, is inhabited by a group of woodpeckers that includes a single breeding pair. Other adults present in the group are typically male offspring from previous breeding seasons (Ligon 1970, Lennartz et al. 1987).

Considerable information is known about the woodpecker's cavity tree requirements. The Red-cockaded Woodpecker requires old living pines for its cavities (Conner and O'Halloran 1987). The presence of fungal decay within the heartwood of pines increases in frequency as pines age and significantly shortens the time required for woodpeckers to excavate nest and roost cavities (Hooper et al.

1991, Conner et al. 1994, Rudolph et al. 1995). A sufficient diameter of heartwood, which increases with pine age, also is required to provide adequate space for cavity excavation (Conner et al. 1994). Pines with suitable cavities are known to be a critical resource for Red-cockaded Woodpeckers (Walters et al. 1992a, Conner and Rudolph 1995). Thus, location of existing cavities and the number and distribution of old-growth pines that can be excavated for cavities likely has a strong influence on the density and spatial distribution of woodpecker groups.

The quality of foraging habitat across the forest landscape also may influence nesting success and the density of Red-cockaded Woodpecker populations. Male and female Red-cockaded Woodpeckers forage at different locations on trees and use different methods to exploit arthropod prey (Ligon 1968, Hooper and Lennartz 1981). Hooper and Harlow (1986) observed that foraging Red-cockaded Woodpeckers showed little preference among pine stands that were more than 30 years old, and concluded that once pine stands reach 30 years old their quality as a foraging substrate does not improve with further aging. More recent studies suggest that old-growth pines provide an increased foraging benefit (Zwicker 1995, Jones and Hunt 1996, Eng-

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strom and Sanders 1997). In this study we evaluate relationships among forest habitat, adult woodpecker provisioning rates of nestlings, and woodpecker fledging success of woodpecker groups where group density is moderate and where group density is low. We ask if foraging habitat characteristics are related to woodpecker group density, nestling provisioning rates, and nesting success. If woodpecker group density is a function of foraging habitat quality, provisioning rates of nestlings where woodpecker group density is moderate might be expected to exceed those of groups living in lower densities.

STUDY AREA AND METHODS

The Vernon Ranger District of the Kisatchie National Forest (31° 01' N, 93° 02' W) is located in west-central Louisiana. Longleaf pines (*Pinus palustris*) compose the bulk of the overstory with grasses and forbs as the primary ground cover. Hardwood midstory vegetation is typically minimal on the Vernon Ranger District but does occur in some areas where the effectiveness of prescribed fire has been reduced. We selected 10 Red-cockaded Woodpecker groups from areas of the national forest where group density was moderate ($\bar{x} = 9.8$ active cavity-tree clusters per 2-km radius) and 10 groups from portions of the Ranger District where group density was low [$\bar{x} = 5.9$ active cavity-tree clusters per 2-km radius; moderate vs low group density: $t_{(18)} = 5.01$, $P < 0.001$; see Hooper and Lennartz (1995) for classification (moderate vs low) of woodpecker group densities]. Prior to the 1992 breeding season, all adult woodpeckers roosting within these 20 clusters were captured at their roost cavities, weighed, and banded with U.S. Fish and Wildlife Service metal bands and combinations of color bands to facilitate individual recognition.

At the onset of the nesting seasons during 1992 and 1993 we climbed cavity trees using Swedish climbing ladders to determine the location of the nest tree, the number of eggs in the clutch, and the initial number of nestlings. During July and August of both years we determined the number of post-fledging survivors for each woodpecker group. We quantified adult provisioning rates of nestlings for each woodpecker group when nestlings were 8, 20, and 23 days old (see Schaffer 1996). The total number of provisioning trips made by adults to feed nestlings was counted during the 3-hour period following the breeding male's initial departure from the nest cavity in the morning. We also identified which adult brought food to nestlings during each provisioning trip and made an estimate of prey size (cm) using the adult woodpecker's bill as a size scale. Nest trees were climbed after each 3-h provisioning sampling period to verify the number of nestlings present in each nest cavity. An adjusted provisioning rate was calculated for each nest by dividing the total number of feeding trips by the number of

adult woodpeckers in the group, yielding the number of provisioning trips per adult. Provisioning rates were also adjusted to simultaneously account for different numbers of nestlings in cavities and group size.

Red-cockaded Woodpecker use of forest stands for foraging depends in part on the distance of the stand from cavity trees (DeLotelle et al. 1987). We measured vegetational characteristics around the geometric center of each woodpecker cavity-tree cluster within three radii: 0–100 m, 101–400 m, and 401–800 m. Forest compartment stand maps were obtained from the Kisatchie National Forest supervisor's office for those compartments falling within 800 m of each cluster studied. Each compartment is comprised of forest stands of varying size and tree age. Five dominant or codominant pine trees were randomly selected as central points in each forest stand, and habitat characteristics for each stand were gathered around each of these five trees. For each stand, means were calculated for each habitat measurement taken around the five central trees.

Stand age was determined by coring each central tree at breast height (1.3 m) with an increment borer and counting the growth rings of the cores. Five years were added to the growth ring counts for longleaf pine to adjust for the minimum years spent as a seedling (Conner and O'Halloran 1987). Stands were divided into five age classes: 0–29, 30–49, 50–69, 70–89, and >90 years old. The diameters of each central tree and of all live stems larger than 2 cm within 11.3 m of the central tree were measured at breast height with calipers. Stands were divided into two diameter classes based on average diameters of pines: 30–40 cm and 40.1–50 cm diameter at breast height (dbh). Pines in smaller diameter classes were excluded because they were rarely encountered. A one-factor metric basal area prism was used to measure pine overstory basal area (m²/ha). Stands were divided into three basal area classes based on average basal areas of overstory pines: 0–3, 3.1–12, and 12.1–21 m²/ha.

Hardwood midstory density was visually estimated and placed into one of five categories: none, sparse, moderate, dense, and very dense. The effects of midstory height (measured with a clinometer) and midstory density may not be obvious when considered independently. For example, tall, dense midstory conditions may have a different impact on the woodpeckers than would tall, sparse midstory conditions. Therefore, both midstory height and midstory density were considered together to obtain measures of suitable and unsuitable midstory conditions. Midstory conditions were considered suitable if the height was less than 3 m regardless of the density, or if the density was none to sparse regardless of the height. Midstory conditions were considered unsuitable if the height was more than 3 m and the density was moderate to very dense.

The area (ha) of each forest stand within distance zones of 100 m, 400 m, and 800 m from each nest tree was measured with a digitizer using Sigma-Scan[®]. The area of each stand was summed for each habitat vari-

TABLE 1. Comparisons of mean (\pm SD) nestling provisioning (feeding) and nest productivity rates between Red-cockaded Woodpecker groups in areas of moderate ($n = 10$) and low ($n = 10$) woodpecker group density on the Vernon Ranger District, Kisatchie National Forest, Louisiana, during the 1992 and 1993 breeding seasons.

Variable	Group density		<i>t</i>	<i>P</i>
	Moderate	Low		
No. feeding trips to 8-day-old nestlings	37.0 (17.3)	37.6 (15.5)	0.61	>0.05
No. feeding trips to 20-day-old nestlings	42.1 (17.5)	43.9 (29.2)	0.19	>0.05
No. feeding trips to 23-day-old nestlings	42.6 (18.4)	46.1 (19.6)	0.06	>0.05
Adjusted 8-day feeding rate	12.9 (7.4)	13.3 (4.0)	0.13	>0.05
Adjusted 20-day feeding rate	14.3 (5.9)	15.5 (9.5)	0.38	>0.05
Adjusted 23-day feeding rate	14.8 (6.3)	16.2 (5.1)	0.57	>0.05
No. adult woodpeckers in group	3.1 (0.9)	2.9 (0.8)	0.48	>0.05
No. of eggs in clutch from successful groups	3.1 (0.9)	2.8 (1.2)	0.80	>0.05
No. of nestlings fledged from successful groups	1.9 (0.9)	1.7 (0.9)	0.67	>0.05

able by age, dbh, and basal area classes as described above for the 100 m, 400 m, and 800 m concentric distance zones around each woodpecker cluster examined and converted to a percentage for each distance zone.

Data were analyzed using SAS (version 6.12; SAS Inst. Inc. 1988) on an IBM compatible computer. Percentage data for stand area in various habitat classes were transformed with an arcsin transformation, and count data for nesting variables were transformed with a square root function to approximate normality in all parametric statistical tests. A stepwise discriminant analysis was used as a data reduction technique to compare habitat variables between groups occurring in moderate and low densities. In order to test the hypothesis that habitat quality influences provisioning rates and woodpecker group density, we calculated two-tailed *t*-tests (adjusted for unequal variances) to test for differences in nest productivity and provisioning effort. Frequencies of nest success, nest attempts, and nest failures for moderate and low group densities were compared with χ^2 analysis using 2×2 contingency tables. Logistic regression (stepwise) was used to evaluate nest success (successful or not) and nest attempts (attempted to nest or not) as a function of habitat characteristics.

RESULTS

Of all habitat variables measured only the percentage area with suitable midstory conditions within 100 m of the nest tree (Wilks' Lambda 0.78, $P = 0.0356$, 1, 18 df) entered the stepwise discriminant function (75% classification accuracy) comparing groups in moderate [$96.3\% \pm 6.5$ (SE) area with suitable midstory] and low ($67.8\% \pm 38.5$) densities, suggesting considerable homogeneity of habitat throughout the Vernon Ranger District. Stands with old-growth pines (pines >90 years old) within 100 m and 400 m of clusters were present around groups occurring in mod-

erate densities ($1.7\% \pm 5.2$ and $2.4\% \pm 5.7$ of the area, respectively) but were totally absent in areas with low woodpecker group densities.

Differences in woodpecker group density did not appear to be a function of foraging habitat quality. We detected no significant differences between moderate and low woodpecker group density in the unadjusted and adjusted rates that adults fed nestlings at 8, 20, or 23 days post hatching, woodpecker group size, clutch size, and the number of young successfully fledged (Table 1). However, the power of our ability to detect a difference is low (5–9%) because of the relatively small sample size ($n = 20$). As with provisioning rates, we failed to detect a difference between moderate and low woodpecker group density in the size of prey that adults fed to nestlings ($t = 0.45$, $P > 0.05$, $df = 24$). The average weight of breeding males was identical in areas of moderate group density (48.3 g) and low group density (48.3 g). Breeding female woodpeckers differed by only 0.1 g, 46.6 g and 46.7 g, respectively.

A significantly higher proportion of woodpecker groups attempted to nest in moderate group densities (19 of 20 nest years) than in low group densities (10 of 20 nest years; $\chi^2 = 10.2$, $P < 0.001$, $df = 1$). Also, a significantly higher proportion of woodpecker groups nested successfully in moderate group densities (17 of 20 nest years) than in low group densities (9 of 20 nest years; $\chi^2 = 7.03$, $P = 0.008$, $df = 1$). The three groups that failed to produce fledglings in the areas with moderate group density were the result of two

nesting attempts that failed and one instance where the woodpeckers did not attempt to nest because the breeding female abandoned the cluster (or died) immediately prior to the breeding season. The 11 groups that failed to produce fledglings in the low-density groups were the result of one attempt (eggs laid) that failed, five instances where the breeding female disappeared immediately prior to the breeding season, and five instances where a pair was present but did not attempt to nest. Two (10.5%) of 19 nesting attempts in areas with moderate group density failed, whereas 1 (10.0%) of 10 nesting attempts in areas with low group density failed ($\chi^2 = 0.002$, $P > 0.05$, $df = 1$). Cluster abandonment by females prior to the breeding season was marginally higher in low group densities (5 of 20 nest years) than in moderate group densities (1 of 20 nest years; $\chi^2 = 3.14$, $P = 0.08$, $df = 1$).

Attempts to evaluate nest success (successful or not) and nest attempts (attempted to nest or not) as a function of habitat characteristics through logistic regression failed as no measured habitat characteristic had a sufficient relationship to enter the analyses.

DISCUSSION

The observed lower rate of nesting attempts in the low-density groups relative to moderate-density groups could be related to at least several factors singly or in combination: (1) failure to nest because of a foraging habitat insufficiency, (2) demographic dysfunction resulting from increased isolation of low-density groups relative to moderate-density groups, and (3) an inadequate number of older-growth pines suitable for nest trees. Inadequacy of foraging habitat appears to be an unlikely explanation. The lack of older-growth pines in the low group density area may have reduced the number of sites available for cavity-tree clusters, and because of increased group isolation, may have had a negative effect on population demographics. Unfortunately, the historic demographics of groups we studied was not known. It is also possible that prey availability, as provided by these older-growth pines, had an influence on cluster abandonment by females and whether groups attempted to nest or not. Limiting factors appear to

prevent nest initiation rather than decreasing the success rate of nesting attempts.

Recent research suggests that Red-cockaded Woodpeckers have a preference for older pines. Zwicker (1995), Engstrom and Sanders (1997), and Jones and Hunt (1996) observed that Red-cockaded Woodpeckers used larger, older-growth pines at much higher rates than would be expected based on availability. However, using logistic regression we failed to detect a relationship between availability of old pines and nesting attempts.

The age and experience of the breeders occupying moderate and low density group areas also may have influenced the observed differences in nesting productivity. Older and more experienced woodpeckers might preferentially capture and occupy habitat with higher densities of older-growth pines because such habitat is viewed as better quality than habitat lacking older-growth pines. The number of young fledged by Red-cockaded Woodpeckers is known to increase with the age and experience of breeders (Walters et al. 1992b). We did not know the ages of the woodpeckers in the groups we studied.

The suitability of hardwood midstory conditions within 100 m of the center of cavity-tree clusters was significantly greater for moderate-density groups, but it was not related to nest productivity or the propensity of groups to nest. The greater presence of unsuitable midstory conditions in areas of low group density than areas of moderate group density suggests that cluster abandonment could also have influenced the observed differences in group density. The Red-cockaded Woodpecker's requirement for open pine stands relatively devoid of hardwood midstory is well known (Conner and Rudolph 1989, Loeb et al. 1992).

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